

P O L S K A A K A D E M I A N A U K
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ACTA PALAEOBOTANICA

MARIA REYMANÓWNA

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CARPATHIANS

Nowy pień bennetyta z Karpat Zachodnich



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DRUKARNIA UNIWERSYTETU JAGIELLOŃSKIEGO W KRAKOWIE

Maria Reymanówna

A Cycadeoidean Stem from the Western Carpathians

Nowy pień bennetyta z Karpat Zachodnich

INTRODUCTION

The silicified Cycadeoid stem which is the subject of this investigation was presented in 1936 to the Physiographic Museum of the Polish Academy of Sciences in Cracow by Professor S. Chmiel, headmaster of the secondary school in Wieliczka. The specimen (Pl. I.) was found by Mr. I. Zając in a stream bed (Text-fig. 1) in the locality Przenosza near Skrzydlina, Limanowa district.



Fig. 1. The stream in Przenosza (Limanowa district), in the neighbourhood of Mr. I. Zając's house. The place where the *Cycadeoidea* was found is marked by a cross

Photo L. Stuchlik

Before the war Dr. J. Lilpop, the Keeper of the Physiographic Museum began the investigation of the stem. Several ground sections were prepared under his direction and also a wedge cut from the apex of the specimen, showing in an excellent way the distribution of xylem and phloem on the radial and transverse section of the stem (Pl. II., fig. 3). Dr. J. Lilpop was also in correspondence with Professor G. R. Wieland of Yale University, USA.

Most unfortunately his work was stopped by the war and afterwards was left unfinished by his premature death.

In 1956 Professor Wł. Szafer was kind enough to entrust me with the description of this specimen.

PART I. GENERAL

1. CYCADEIDS FOUND IN POLAND

The investigation of Polish Cycadeids has a long history although only a few specimens have been found.

The first small fragment was found in 1746 in a swamp at Lednica, near Wieliczka, South East of Cracow. Judging from E. I. Walch's drawing in H. Jähniczen's paper (1956) it bore a flower bud. What happened to it afterwards is not known.

In 1753 (or little earlier) M. Borlach, then Counsellor of the Salt Mines at Wieliczka sent to the „Naturalien Cammer” at Dresden a huge *Cycadeoidea* stem. Like the first fragment it was found in a swamp near Lednica. This fossil was described in 1853 by H. R. Goepfert as *Raumeria Reichenbachiana*.

In the early thirties of this century Professor R. G. Wieland was able to reinvestigate the stem thanks to the initiative of Professor R. Kräusel. Professor Wieland made a series of ground sections and gave an accurate description of the structure shown by the stem and flowers. Fortunately this Cycadeid proved to be excellently preserved, and, what is more, to bear male flowers containing mature pollen grains, which does not happen often.

In 1844 a third Cycadeid fragment was described by H. R. Goepfert as *Raumeria Schulziana*. It was found in pleistocene gravels near Gliwice during the excavation of the Clodnitz canal. This specimen is now in the Palaeobotanic Museum of the University of Wrocław.

In 1897 a Cycadeid stem found somewhere in the Carpathians was described by M. Raciborski as *Cycadeoidea Niedźwieckii*. Thanks

to the initiative of Professor Wł. Szafer a drill core from this specimen was sent to Professor R. G. Wieland by Dr. J. Lilpop. The sample contained an immature female cone of elongate shape. The flower had probably possessed stamens which were already shed before fossilization. Professor Wieland is of the opinion (1941, p. 525) that „There is in preservation and type a remarkably close parallel to the „Fossil Cycad National Monument” series of specimens from the Black Hills (Dakota, USA), which are of Lower Cretaceous Age.

In 1925 a further specimen was found by K. Wallisch, on pleistocene gravel near Kamień, in the district of Nisko, and described as *Cycadeoidea polonica* (K. Wallisch, 1928). The two last mentioned specimens are now in the Museum of the Polish Academy of Sciences in Cracow.

2. THE PROBABLE ORIGIN OF THE CARPATHIAN CYCADEOIDS

At the moment five Cycadeoids are known from the Southern part of Poland, but not one of them was found „*in situ*”. The origin of these fossils is an exciting problem for the Polish palaeobotanists and geologists who have searched the concerned area many times but without result.

As early as 1893 M. Raciborski had supposed that somewhere in the Carpathians occurs a layer rich in Cycadeoid stems, probably a cherty one. Foreign palaeobotanists too, were interested in that supposition. Professor Bertrand of Lille wished to search in Poland himself and there are many statements of Professor G. R. Wieland who believed that in the Carpathians exist layers containing Cycadeoids in profusion; layers similar to the American ones and, like some of them, probably bearing also dinosaurs.

In the autumn of 1958 the author made a search in Przenosza in the company of Dr. J. Burtan who made the geological map of the area. But no strata containing Cycadeoids nor new specimens were found. Professor S. Chmiel too, had searched here for many years without result. The Lednica area near Wieliczka which produced *R. Reichenbachiana* was also examined. The bed of the stream flowing from the Chorągwica Hill in the direction of the main road was investigated and some outcrops nearby were examined without finding any specimen. According to M. Borlach (H. Jähnichen, 1956) the fossil was found in a swamp near a stream. In the neighbourhood the substratum consisted of shaly clays, but there were other kinds of rock too.

Considering the problem of the origin of the Polish Cycadeoids we have also to bear in mind the differences in their fossilization. These fossils may be divided into two groups:

I. The red specimens found beyond the Carpathians lying on alluvial deposits (*R. Schulziana*, *C. polonica*). At the moment it is difficult to suggest anything about their origin, but as their way of preservation differs from that of the second group, their source rock may prove a different one.

II. The black specimens (*R. Reichenbachiana*, *C. Niedźwiecki*, *C.* from Przenosza) found in the Flysch area of the Polish Carpathians. We know only the localities where two of them were found: Lednica near Wieliczka (*R. Reichenbachiana*) and Przenosza (*C. sp.*). According to Dr. J. Burtan the rocks occurring in these areas are of various origin. We may find there:

1) Erratics deposited by the moving ice which are found around Wieliczka. One of K. Wallisch's suppositions concerning his *C. polonica* was that its source was eroded material carried forward by the ice sheet. This possibility is to be excluded at least in the case of *C. sp.* from Przenosza as the locality is beyond the reach of both the Cracovien (Mindel) and the Tatra glaciations (Text-fig. 2).

2) In both areas the Flysch deposits contain foreign rocks, mostly palaeozoic or light grey Jurassic deposits and igneous rocks. It does not seem very likely that they yielded the Cycadeoids.

3) In all probability the Cycadeoids come from the Flysch deposits themselves which consist of Cretaceous and Palaeogene strata. Only the Cretaceous ones may be considered as we do not know any Tertiary Bennetites.

There are some data available pointing to the fact that the Barremian Verovice Shales („łupki wierzowskie”) might be the source of the Cycadeoids. The „Verovice beds” are black shales, clayey, limey or a little silicified, with bands and nodules of siderite” (M. Książkiewicz, 1951 p. 92), containing in some places rich ammonite faunas. The first fact indicating that they may contain Cycadeoids is that fossil plants were found in them. Dr. J. Lilpop (1957) mentions in his textbook „the rich flora known from the Verovice Beds in Moravia, close to the Polish border”. A. Schenk (1871) describes that „rich flora consisting mainly of *Cycadeae* and indicating a tropical climate”.

From the similar dark shales of the Grodischt Beds (Barremian) a petrified conifer wood has been described (M. Reymanówna, 1956). It was presented to the Institute of Botany of the Polish Academy of Sciences by Professor M. Książkiewicz. The Cycadeoids are also petrified and this kind of preservation does not occur frequently.

A further hint may be the kind information of Dr. T. Wieser that both the colour and the mineral content (mainly silica, iron-pyrites) of the Przenosza fossil recall strongly the dark Verovice Shales and also Lgota Shales (Aptian-Albian).

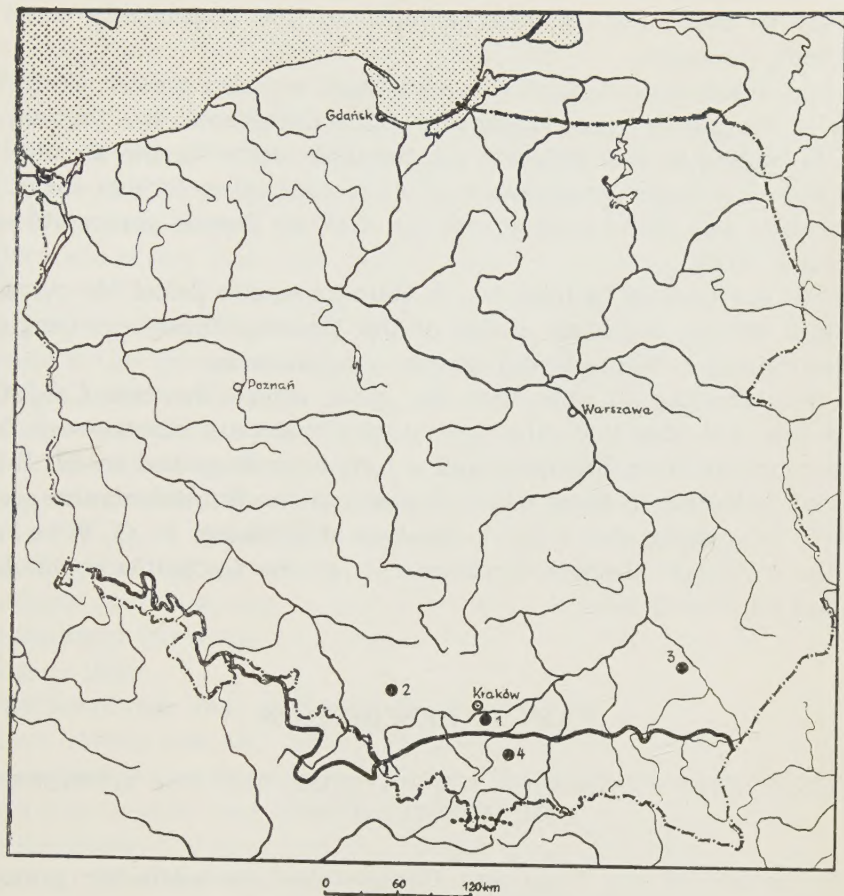


Fig. 2. The localities in Poland where *Cycadeoids* were found.
 — border of the area covered by the Cracovien-Glaciation
 border of the area covered by the Tatra-Glaciation (both
 according to M. Klimaszewski, 1952)

Another indication comes from Dr. J. Burtan who has been investigating for several years the geology of the environs of Lednica and Przenosza. She was kind enough to give me the information that the Verovice Beds occur in both these areas. According to Dr. Burtan, in the Przenosza area, above the place where our fossil was found, there occur several Cretaceous deposits. There are Grodischt Beds consisting of layers of sandstone, black shales, clayey and marly shales with bands of siderite and marls. An outcrop of the Cretaceous strata may be seen in the stream bank, some 20 metres up from the spot where the *Cycadeoidea* was found. It should be emphasized that the fossil shows many cracks

and may be easily split with a hammer, so that it probably could not stand long transport.

In the Inoceramus Beds of this area there are also present Cretaceous strata of the biotite type. Lying above the Cretaceous are Tertiary deposits belonging to two different stratigraphic units. In the Menilite top series lenses of coarse conglomerates occur containing foreign rocks. Our *Cycadeoidea* was found loosely and „*ex situ*” on Eocene glauconite sandstones and shales.

In the environs of Lednica Dr. J. Burtan also found Verovice and Grodischt Shales; the black shales of the Verovice type bear conglomerates containing calciferous and igneous foreign rocks.

It is interesting to note that the spots where the two Carpathian Cycadeoids and also two other petrified Cretaceous plants were found (*Araucarioxylon* from Stempina and a fern stem described by M. Raciborski, 1915) lay in areas where deposits of the Sub-Silesian nappe are exposed. Interesting also is the suggestion of Professor R. G. Wieland that the Northern Mesozoic-Tertiary rim of the Carpathians should be searched for Cycadeoids.

PART II. DESCRIPTION

1. THE PRESERVATION OF THE MATERIAL AND THE METHODS OF INVESTIGATION

The tissues of the Przenosza *Cycadeoidea* are perfectly preserved although not throughout the specimen. The substance contributing mainly to the fossilization was silica, sometimes also calcite. The bracts and leaf-bases bear white calcite margins and calcite veins also occur, mainly in the cambium zone. In some parts there is a considerable amount of iron-pyrites and there the cellwalls are rather poorly preserved. Some tissues decayed before fossilization, e. g. the outer parts of the leaf-bases which consist often only of a dark matter, showing no cell structure.

Preparations revealing the microscopic structure were made in several ways. A big wedge showing the distribution of the vascular tissues on the transverse and radial section of the stem was prepared at the time of Dr. J. Lilpop. These two surfaces were polished and etched with hydrofluoric acid to allow good observation. (Pl. II, fig. 3). Dr. J. Lilpop also left some ground sections, but their small size made investigation difficult. The author used ground sections only on a few occasions where the damaged tissues were supposed to appear more distinctly than on peel sections.

Some seventy peel sections were prepared in Scotland, in the Laboratory and under the direction of Professor John Walton, Department of Botany, Glasgow University and afterwards in the Palaeobotanical Laboratory, Institute of Botany, Polish Academy of Sciences, Cracow.

Using the Peel Section Method of Professor John Walton (1928) very good results were obtained. The procedure was as follows: The surface of the petrification was ground smooth on a glass plate with carborundum and water and then etched with concentrated hydrochloric acid (HCl) for one minute, washed with water and etched with concentrated hydrofluoric acid (HF) for about one minute. The HCl was used in order to remove the calcium carbonate (CaCO_3) which produces with HF the insoluble calcium fluoride (CaF_2). This compound may spoil the preparations, especially when a series is to be taken (comp. J. Walton, 1923). After washing and drying a solution of cellulose nitrate in amyl acetate was poured over the surface. When dry the mixture forms a film which after being pulled off represents a very thin section of the fossil tissue. Some of the sections were mounted in balsam under a cover slip, the others are preserved in bags and boxes but the best way is to put them between the leaves of a book to keep them flat (comp. M. Reymannówna, 1960).

The simplified Peel Method of K. W. Joy, A. J. Willis and W. S. Lacey (1956) was also used. The surface of the petrification was prepared as before. Some acetone was then poured on, a piece of cellulose acetate film applied and when dry pulled off as in the first method. For finer structures the first method proved more convenient.

It must be said that the Cycadeoid stem as it contained a mixture of silica, calcite and iron-pyrites was not the best material for applying the Peel Method which produces the best results with calcite or silicified petrifications. Nevertheless the preparations were good and their size much greater (about 1 sq. decimetre) than that of the ground sections. Only by using this method was it possible to make series of 20 or 30 sections of one flower bud (see text-fig. 5A—F).

Using maceration in HF fragments of rammenta were isolated (see Pl. IV, fig. 11—13).

2. DESCRIPTION OF THE CYCADEOIDEA STEM

a) Macroscopic features

The fossil is part of a stem apex, dark grey in colour (black when polished), 25 cm. high and about 35 cm. in diameter at the base. The

breadth of the armour consisting of persistent leaf-bases covered densely with scaly hairs (ramenta) is 7—8 cm. (near the stem base). On the apex the armour is not preserved, apparently having been destroyed before fossilization. The lower part of the specimen has been broken off, as well as a piece on one side. But there is no evidence of long transport by water.

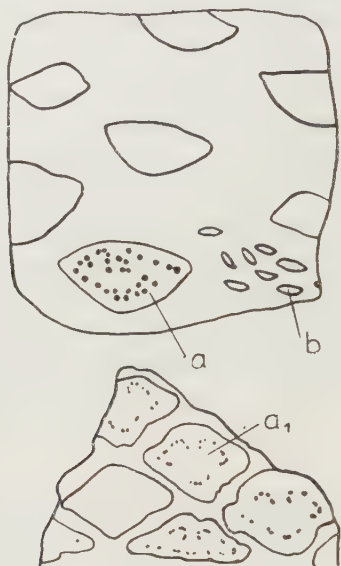


Fig. 3. The pattern of the bundles in leaf-bases of *Cycadeoidea* from Przenosza. a) some bundles are doubled, a₁) the pattern found in most *Cycadeoids*, b) bracts. nat. size

On the right side of the picture (Pl. I, fig. 1) there may be seen cavities left by the shed leaves and bracts, also some flower buds, and the uneven surface of the spaces filled with ramenta are visible. In many places a dark cracked matter, something like resin, is present. On the left side the unevenness of the surface is covered by a precipitated iron compound. Here the floral buds are often damaged and their summits are lacking.

The shed leaves were cut off by an absciss layer of cork (Pl. II, fig. 5) which formed about 1 cm. beneath the armour surface. The resulting cavity surrounded by ramenta preserves the shape of the shed leaf-base just as if the ramenta were glued together.

The transverse section of a leaf-base is lozenge-shaped, ranging from 10—16 mm. in width (av. 13 mm.) and from 6—9 mm. in height (av. 7 mm.). Approaching the surface of the armour the dimensions gradually become smaller (Pl. II, fig. 3).

The stem bore leaves arranged in spiral order, but the pattern was disturbed by numerous flower buds. These are mostly small and difficult to see. Their diameter is 1,5—4 cm. and they are usually surrounded by a few bracts measuring $4 \times 1-2$ mm. There are also some bigger cavities in the armour, left probably by shed flowers.

b) Microscopic structure

In the centre of the stem is a large pith surrounded by a ring of xylem and phloem about 1 cm. wide, succeeded by a cortex of 2 cm. (Text-fig. 4, and Pl. II, fig. 3).



Fig. 4. The transverse section of a fragment of the *Cycadeoidea* showing the distribution of the phloem and xylem and the bundles going through the cortex. a) pith, b) xylem, c) phloem, d) bundle in the cortex, e) armour. (Drawing from a photograph) about nat. size

The pith consists of thin-walled, cylindric cells whose longer axes lie parallel to that of the stem (Pl. IV, fig. 14). They are ranging from 122—320 μ in height (av. 235 μ) and from 49—230 μ in diameter (av. 122 μ).

Between them small intercellular spaces are visible. Some of the cells are filled with a dark substance appearing to be similar to the content of the „gum” ducts. In some cells small oval bodies occur and often fungal hyphae are to be found.

In the parenchyma of the pith, cortex and leaf bases „gum” ducts are present. They are globular spaces ranging from 260—500 μ in diameter (av. 370 μ) surrounded by a layer of flat cells, and usually several of them form together a canal. The ducts often bifurcate in the shape of the letter Y this being seen very often on the transverse section of the pith.

In the pith there are no vascular bundles as in the pith of some of the *Cycadaceae*. But there are present layers consisting of flat cells which were described by M. R a c i b o r s k i (1893) and K. W a l l i s c h (1928) as cork and by G. R. W i e l a n d (1906) as „internal periderm”. In the same part of the pith there are groups of decayed cells filled with a dark substance.

The phloem and xylem were investigated by means of preparations taken 10 cm. beneath the stem apex. They form a ring showing gaps in places where bundles pass through to the leaves and buds (Pl. II, fig. 4). Growth rings were not observed.

The xylem is much worse preserved than the phloem and it is not even possible to tell its breadth. In many places scattered wood fragments and coprolites are seen which would suggest destruction by unknown organisms. Also in the bundles which pass through the cortex the xylem is poorly preserved. The inner part of the xylem consists of small radially seriated tracheids ranging from 20—29 μ in tangential diameter (av. 23 μ). The same diameter of the medullary ray cells is much greater ranging from 44—78 μ (av. 58 μ) (Pl. III, fig. 7). The outer part of the xylem consists of regular radially seriated tracheids of rectangular shape, ranging from 29—44 μ (av. 37 μ) in radial and from 15—34 μ (av. 26 μ) in tangential diameter. Medullary rays occur after every 1—4th row of xylem tracheids. The rays consist of one row of cells, sometimes partially of two, and the cells are of the same diameter as the tracheids.

On the radial walls of the tracheids flat single or double pits occur, sometimes also round pits being present (Pl. III, fig. 10).

The cambium is mostly visible as a black line resulting from the collapse of the tissue. But in a few places the cambium is well preserved and there about four layers of cells with thin, shrivelled walls can be seen (Pl. III, fig. 8).

The phloem is well differentiated from the xylem by the dark colour due to the organic compounds filling the cells. The phloem consists of thick-walled fibres and thin-walled vascular elements (Pl. III, fig. 8). Also in the phloem the medullary rays which are near the cambium are

of the same breadth as the phloem cells, but on the outside they become much wider. Here the phloem elements measure from $10\text{--}29\mu$ (av. 18μ) and the ray cells from $34\text{--}69\mu$ (av. 48μ) in tangential diameter (Pl. III, fig. 9).

The vascular bundles coming from the gaps in the stele pass through the cortex and go directly to the leaf-bases (Pl. II, fig. 3). They form an angle of about 45° with the stem axis. They start as single horse-shoe-shaped bundles which divide into 3—5 parts, becoming fan-shaped and finally circular (Text-fig. 4). Before entering the leaf-base they divide into about 30 small bundles which bifurcate afterwards in the leaf itself.

The stem and the leaf bundles are covered with several (up to 12) layers of flat cork cells. The epidermis is poorly preserved. It is covered with densely packed scales with short marginal hairs (ramenta). In many places the epidermis became separated from the underlying tissues before fossilization, and the crack is filled with white calcite.

The parenchyma and the „gum” ducts of the leaf-bases consist of smaller elements than these tissues in the stem. The length of the parenchyma cells is ranging from $123\text{--}368\mu$ (av. 216μ), their breadth from $74\text{--}157\mu$ (av. 103μ) and the „gum” ducts are from $190\text{--}390\mu$ (av. 280μ) in diameter.

On the transverse section the bundles are arranged in a semicircle with inturned margins (Text-fig. 3a¹). This pattern is characteristic for the great majority of Cycadeoids. Sometimes the bundles are doubled, probably where the section has passed at a level where the bundles were bifurcating (Text-fig. 3a). A similar pattern may be seen on G. R. Wieland's picture concerning *Raumeria Reichenbachiana* (1934, Pl. X, fig. 3). According to K. Wallisch (1928) the pattern of double bundles is a characteristic feature of *Cycadeoidea polonica*.

On the transverse section of a leaf bundle several radially seriated tracheids of the centrifugal xylem are seen (Pl. II, fig. 6). There are also protoxylems and some large elements are situated inside the protoxylem which might suggest that they belong to the centrifugal xylem. The tissue outside it, where phloem is to be expected, is not preserved. The vascular tissue consists of tracheids bearing spiral thickenings, or having scalariform or round pits. The entire bundle is surrounded by a sclerenchymatous sheath consisting of cells with dark content.

The ramenta. The surface of the leaf-bases, peduncles and bracts is covered with narrow, elongated scales (ramenta). They were investigated on ground sections and peel sections, and also fragments about 1 cm. in length were isolated by maceration in HF (Pl. IV, fig. 11—13). The ramenta are straight or curved, those which grow on the bracts of the immature flower buds being particularly curved.

The ramenta are elongated scales 140—700 μ wide, 40—140 μ thick and spindle-shaped on the transverse section. The ramenta covering the bracts consist of one layer of cells, but the others have one to four layers. In the macerated material occur wide and thick and also narrow and thin fragments. It would appear that these last are the summit parts of the first ones.

An isolated ramentum resembles a harpoon because its edges bear short, stout projecting hairs. Seen from the flat side of the ramentum they appear to be triangular cells with a spine on the top. The cells are empty or they contain a dark substance which occurs also in the canal which is sometimes visible in the spine. It seems quite possible that the substance is the same dark matter, the „gum” or „resin” found in the many ducts in the parenchyma throughout the whole stem. Sometimes the cells become longer, and on some fragments belonging apparently to the ramenta-bases there occur long hairy outgrowths (Pl. IV, fig. 12).

Perhaps the spiny ramenta which were probably glued together could protect the plant to some extent from damage caused by insects or other enemies. Such damage is frequent and will be described later.

Recent Ferns, especially Tree-Ferns, bear scaly ramenta, but the recent Cycads have only scarce filamentous hairs on the stem. The fossil Cycadeoids bore masses of ramenta. They formed together with the persistent leaf-bases a stem protecting armour. This well protected stem may suggest that the plant was living in very dry and hot climate.

c) Flower buds

It seemed at first that the *Przenosza* Cycadeoid did not possess flowers at all. But already the first sections revealed bracts. Close observation of the armour showed that there are many traces of shed bracts, indicating bud apices. But they are not easy to find and it is difficult to establish the real position of a bud. This is caused by the small size and number of the bracts. The *Przenosza* stem differs in this feature from the great majority of the Cycadeoid stems described hitherto whose buds are surrounded by a large number (up to 150) of quite distinct bracts.

Sections from 12 flowerbuds were studied but the buds III, V and XV proved to be the most interesting ones. (The objects supposed to be flower buds, judging from their outer appearance, were numbered with Roman numerals. After sectioning it turned out that some of them were not buds at all, but it was more convenient not to change the markings). Using the peel method a series of 34 longitudinal sections was made from bud V and 21 similar preparations from bud VI. The sections give a good idea of their macroscopic and microscopic structure.

As can be seen on the pictures (Text-fig. 5A—F, and Pl. V, fig. 17) bud VI did not produce sporophylls. Crowded bracts, bending inwards and protecting the interior of the bud, are situated on the peduncle. They bear curved ramenta. The sterile bud XIII looks very similar.

A layer of cork is visible below the apex of bud VI (Pl. V, fig. 19). This structural detail indicates that the bud was not able to develop any more. A ring of phloem and xylem is present in the peduncle. The xylem consists of elements with scalariform thickenings, but also pitted tracheids occur, and in the parenchyma of the peduncle occur „gum” ducts, just as in the pith of the stem and of the leaf-bases (Pl. VI, fig. 26).

In bud V the apex is lacking (Fig. 6A—F). Contrary to the former bud, its bracts go straight upwards. On the top of the peduncle there is a cup-like hollow about 8 mm. deep (Pl. V, fig. 16, 18). A cork layer about 15 cells thick is situated about 6 mm. below that hollow (Pl. V, fig. 20). On the top of the cork there is a few mm. thick layer of parenchymatous tissue with not very distinct cell walls, which contains quite a lot of a secretion. A second, thinner cork layer occurs above. It is succeeded first by a zone of isodiametric thin-walled parenchymatous cells and then by several layers of oblong cells. Towards the top the cell walls seem to disappear gradually and the cells seem to contain more and more secretion. The bottom of the cup-like hollow is covered by probably the same dark secretion which occurs in the „gum” ducts (Pl. V, fig. 21). On some preparations an isolated piece of that matter is to be seen above the hollow (Pl. V, fig. 16). Bud XI, situated on the upper part of stem, is closely similar to the former one in its features. It is the largest and probably also the oldest flower bud. Unlike the others it is quite easy to distinguish on the stem surface as a small, sideways flattened cone, 4 and 1,5 cm. in diameter, bearing a few traces of bracts.

On the transverse section of this bud, 3,5 cm. below the stem surface, only bracts are visible (Pl. VI, fig. 23). On the next section 3 cm. below, is visible also the peduncle which is $3 \times 1,5$ cm. in diameter (Pl. VI, fig. 24).

This peduncle shows well preserved parenchyma and a ring of xylem and phloem. Some areas are filled with scattered fragments of tissue, in all probability produced by some animals (insects?) feeding on them.

The longitudinal section through the part of the bud lying between the two transverse sections bears a close resemblance to that of bud V (Pl. VI, fig. 25). On the top of the peduncle a cup-like hollow is visible which, as in the former one, is covered by a layer formed of dark secretion. Below occur strata of cork which in this particular case do not show their structure very well. Also a loose piece of the dark substance is visible here.

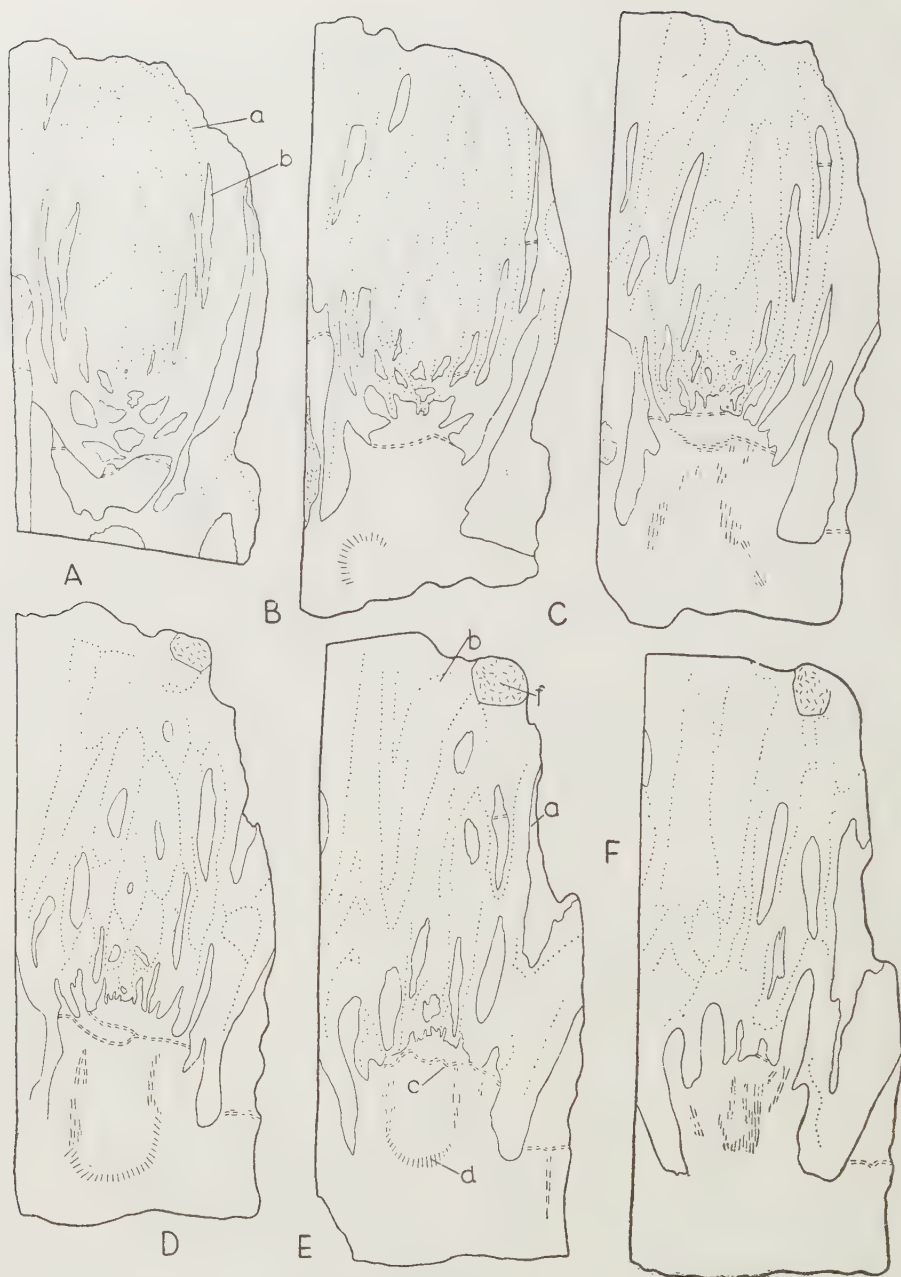


Fig. 5A—F. A series of longitudinal sections of the undeveloped bud VI. (Drawings from photographs of a series of peel sections). a) lines — outlines of the peduncle and bracts, b) dotted lines — probable borders of the neighbouring bracts (of their ramenta), c) cork layers, d) vascular bundles, e) gelatinous tissue and secretion, f) areas damaged by insects. Slightly reduced.



Fig. 6A—F. A series of longitudinal sections of flower-bud V with aborted apex.
lettering as in Text-fig. 5, nat. size

It is possible that in this bud as well as in the former one the apex was shed before the seeds were ripe. The cause of the abortion was probably destruction caused by insects (?). The longitudinal section of bud XVI resembles closely that of buds V and XI.

The longitudinal section of bud XV bears interesting supplementary features. This bud situated at the base of the stem, is 7.5 cm. high and the only parts of it visible on the surface are a few bracts. The bud consists of a peduncle 3 cm. in length with a hollow at the top and of the abortive upper part, separated by a narrow breach from the peduncle. Its lower part corresponds to buds V and XI. The bottom of the cup-like hollow is covered with a 4 mm. thick layer consisting of secretion, which is separated by a cork layer from the parenchyma situated below. The rim of the hollow has uneven edges which may suggest that they were torn away from the corresponding part of the aborted bud. A similar structure occurs also in buds V and XI (Pl. VI, fig. 22).

The abortive upper part of the bud consists of a peduncle about 1 cm. in length bearing a set of bracts, succeeded by the bases of the stamens („campanula”), and an immature female cone on the top (Pl. VII, fig. 29).

The base of the abortive part showing no cell-structure fits in the hollow of the peduncle below. The rest of the aborted peduncle shows cell-structure and in the parenchyma branching vascular strands are visible. The bracts go straight upwards and they do not form a dome closing the bud as in bud V.

The features observed in buds VI, XI and XV give us an idea of the process of the abortion of a bud. Probably at the first stadium one or several cork layers were formed, which finally also cut the vascular strands. A few mm. above the degeneration of the parenchymatous tissue began. The cell walls disappeared gradually and the cells became filled with a dark substance. At this weakest part of the peduncle the immature bud was broken off. The exposed tissue became covered with the dark secretion produced by the „gum” ducts and the parenchyma cells themselves (Pl. V, fig. 21). The aborted flower bud was possibly quite similar to the specimen found in Scotland of *Williamsonia scotica* Seward (R. G. Wieland, 1916, v. II, p. 193).

A picture of a similar bud which is about to be shed can be seen in G. R. Wieland's work of 1916, Pl. 27, fig. 5. In this bud some layers of different tissues are situated below an immature female cone. Being of semicircular shape they resemble the top of the peduncle in buds V, XI and XV. G. R. Wieland's (l. c.) suggestion was that these were periderm layers and their existence may have resulted in the shedding of the cone. According to him, this absciss zone occurred often in very young fructifications, which would probably be aborted — or in ripe ones.

The longitudinal section of the bud of *C. polonica* (see K. Wallisch, 1928, Pl. 10, fig. 2) bears a striking resemblance to buds V, XI, and XV. There the tissues are not so well preserved but a distinct cork band outlining the cup-like hollow on the top of the peduncle is to be seen. There are also some more cork layers below.

Buds I, VII and VIII were sectioned only at a level about 4 cm. below the stem surface. As the sections showed only bracts, in all probability the essential parts of the bud were aborted and therefore no further examination was made.

Also peduncle IX lacked its summit. The peduncle is seen to have well preserved parenchyma in its cortical regions (Pl. VII, fig. 27). It is succeeded towards the centre by a ring filled only with crystalline mineral matter and then by a zone of more or less preserved fragments of vascular tissue. The centre is filled with a dark probably gelatinous substance showing no cell-structure at all.

There are more flower buds on the stem which were not investigated, but their small size suggests that probably all of them were immature or abortive.

Bracts. Generally they have no distinct cell structure, except the outer few layers of cork. Their inner part is filled up with large „gum” ducts, surrounded by a dark substance where mostly no cell walls are evident.

Only the inner bracts of bud XV show well preserved structure (Pl. VIII, fig. 34a). Their abaxial part consists of several layers of thick-walled cells showing a round transverse section (comp. G. R. Wieland, 1906, pp. 115—116). The adaxial part consists of parenchyma containing „gum” ducts and 3—5 vascular bundles.

The female fructification. The female cone of bud XV seen in tangential section is of oval shape, 14 mm. in length and 9 mm. in width. From the transverse section it is evident that its maximum length was about 18 mm., and the diameters 17 and 19 mm. The cone stands on the top of the peduncle. Above the wide base two small outgrowths are seen. The upper half of the cone is covered with a 1 mm. thick layer corresponding to that of ovules and interseminal scales in mature fructifications. The apex of the cone is not preserved, it was presumably damaged by insects feeding on it. This upper part of the cone is cut off by a sharp, irregular line, and outside there are only scattered fragments of smashed tissues.

Figure 32 (Pl. VIII) represents the transverse section of this fructification. In some spots the tissues are torn, probably because the cone became flattened, but they are in general well preserved. The centre is partly empty, partly filled with a secretion and it is surrounded by a ring

of vascular bundles, sometimes joined together. The parenchyma lying outside is interwoven by numerous small bundles, going to the ovules and interseminal scales. These bundles consisting of scalariform elements are seen both in transverse and longitudinal sections.

The stratum of scales and ovules is damaged in many places, but there are spots where groups of round, thin-walled cells, often with brown content, are seen (Pl. VIII, fig. 33 and Pl. IX, fig. 35). Perhaps these belong to young ovules and the surrounding elongate cells with thicker walls belong to the interseminal scales.

The microsporophylls. On the longitudinal section of the same bud can be seen two outgrowths, widening towards the top, situated on both sides at the base of the female cone. They are cut off at the same level as the apex of the cone (Pl. VII, fig. 28). At first they may be taken for the uppermost bracts. But an examination of the transverse section of this bud (Pl. VIII, fig. 32) makes it evident that they belong to the „campanula” consisting of bases of microsporophylls joined together (G. R. Wieland, 1934).

This structure is characteristic for *Cycadeoidea* flowers in the polliniferous stage. The microscopic structure of the „campanula” is not clear, but we may distinguish the basic tissue consisting of small brown cells and the scattered yellow bundles (Pl. VIII, fig. 33). The upper part of the microsporophylls could not be examined because they were destroyed, probably by insects. A proof of this may be the fact that the entire upper part of the bud surrounded by bracts is filled with débris of tissue. As the bud is dilated and open and there are in some spots structures resembling microsporangia, it is quite possible that the microsporophylls were not shed off from the bud, but were destroyed inside and in an immature stadium. If not they would be broken off much nearer their base.

Several preparations were made from the bud at different levels, but no better preserved parts of microsporophylls were found. It was not even possible to find out their number (Pl. VII, fig. 30).

In bud III better preserved fragments of microsporophylls were found. This bud reveals some interesting features, but it is not very well preserved and is very difficult to interpret. This bud was visible on the stem surface as a small eminence which showed after grinding, structures resembling the rows of „synangia” described in *Cycadeoidea*.

On the transverse section from a lower level there are seen quadrangular agglomerations of pollen-like bodies forming parallel rows about 0,6 mm. high. (Pl. IX, fig. 36). On the ground section the areas round these agglomerations corresponding to „synangial walls” are empty, but on the specimen they are filled with iron-pyrites destroyed by grinding.

Above each row of „synangia” there is a thin band consisting of small cells and containing vascular bundles. The bands are supposed to be vascular bundles in the microsporophyll. In some places there is evidence that the „synangia” are connected with them. In the same section an area filled with destroyed tissue is seen.

On the next ground section (Pl. IX, fig. 37) a more complicated picture can be seen. Some tissue, belonging probably to the axis of a microsporophyll, is seen on one side, and on the opposite side there is a series of lateral branches bearing „synangia”. There occur also some sterile branches and a fertile one, all of them having a common basis. There are also four other sterile branches with apices turning toward the centre.

The third and lowest section shows only the contours of a squeezed and folded body. Next to them there are seen two small bract-like structures.

The pollen grains. The great majority of pollen grains are associated in tetrads which form together large agglomerations. Their shape resembles that of the spores in the „synangia” of the genus *Cycadeoidea*. But also single spores occur. (Pl. X, fig. 41). Small parts of the archesporium including tetrads are preserved only in a few places.

The long axes of the four pollen grains in a tetrad are parallel. The pollen grains are mostly connected at both apices, but sometimes at only one. Their equatorial part is bent outwards and for this reason the flattened lensiform spores are often of a boat-like shape (Pl. IX, fig. 39) with sharply pointed ends. The length of the pollen grain is about 18μ and the membrane is rather thick, brown. Sometimes a longitudinal furrow seems to be present.

The *Cycadeoidea* pollen grains found by G. R. Wieland in *C. dacotensis* (1906) and *R. Reichenbachiana* (1934) measured about 70μ (judging from the figures). They were spindle-shaped and had a longitudinal furrow. The small size of the pollen grains of the *Cycadeoidea* from Przenosza may be explained by their immaturity. This is proved by the fact that they are still in tetrads.

Bud III is probably an abortive one and therefore a not fully developed male part of the flower. This is suggested by the presence of pollen grains, forming groups, recalling the „synangia” in the *Cycadeoidea* flowers. This interpretation seems to be correct, although there are several weak points in it. They are as follows: The *Cycadeoidea* from Przenosza has, as was mentioned already, pollen grains of strikingly small size (18μ), compared with the big spores described by G. R. Wieland. The furrow is not easily distinguishable and the pollen-membrane is rather thick with some thinner spots. The arrangement of the branches of the microsporophyll is not clear while in most of the known male *Cycadeoidea* buds the micro-

sporophyll forms a regular star-like pattern. Presumably the bud underwent deformation owing to insects feeding on it. This was probably also the reason why bracts are lacking.

d) Traces of insects

Damage caused by some animals, presumably insects, is a characteristic feature of the investigated stem. It is frequent and occurs in several places and in different tissues. However the parenchyma, containing „gum” ducts, and the phloem are usually undamaged.

The xylem on the other hand shows great damage, and for this reason it is mostly very narrow (comp. Text-fig. 4) and is accompanied by irregularly scattered debris of tissue. Sometimes one may observe burrows eaten out in the wood. These are also frequent in the ramentum coat of the stem.

There occur also greater damage extending over several neighbouring ramenta (Pl. X, fig. 42). Some stretches were so much damaged that after maceration only small fragments of ramenta were obtained.

The noxious insects were particularly fond of flower buds. They burrowed into in the xylem of the peduncle, in the neighbouring tissues (Pl. VI, fig. 24), or in the bud itself where they attacked mainly the female cone with ovules and the microsporophylls. Therefore in the previously described bud XV the microsporophylls were completely destroyed and in bud III we may observe burrows going through the spore-masses. The burrow on fig. 40, (Pl. X) is narrow at the beginning, does not change its width for quite a long stretch, and then suddenly widens. The walls of the corridor consist of damaged pollen grains.

The destroyed areas may attain quite large dimensions, e. g. in the upper part of bud XV there occurs one measuring 25×20 mm. Such areas are filled with loose debris of the neighbouring tissue. (Pl. X, fig. 43). Oval bodies, probably coprolites, were also found. Sometimes they form bigger masses (Pl. X, fig. 42).

The activity of the noxious insects must have produced a reaction of the plant. It expressed 1° in the increased secretion of the „gum” and the tendency to turn the parenchyma into a structureless secretion, 2° the tendency to produce absciss layers and, in connection with this, the abortion of those parts of the plant which were attacked by the insects. Loose „gum” particles occur also on the surface of the stem and inside it, close to the damaged tissues. The parenchyma becomes „gelatinous” in the peduncles (comp. pp. 11, 12) and often in the bracts next to the cork layers. These layers cut off the apices of flower buds and occur also at several levels in the leaf-bases, bracts and even in the pith of the stem.

The pathological state of the plant is manifested of course in its external features. The surface of the stem and the pattern of the leaf-bases and flower buds is not so regular and distinct as on other Cycadeoid stems.

The fact that the insects fed both on female and male parts of the flowers may lead to some further suppositions.

It is a fact known, that when insects feed on male and female flowers they transport at the same time the pollen to the ovules. For instance G. R a t t r a y (1913) observed that the pollination of the Cycad *Encephalartos villosus* L e h m. is carried out by insects belonging to *Rhynchota*, feeding on pollen; their females lay eggs on the ovules in the female flowers. In this way the pollination is secured although some of the ovules are destroyed by the larvae.

It is rather doubtful whether in our case such an advanced state of symbiosis existed, because the facts seem to indicate that the flowers aborted when in a very immature state. It is possible, however, that what we observe here may be a state leading to symbiosis which culminated in other groups of plants in forming the insect-pollinated flower.

3. THE SYSTEMATIC POSITION OF THE CYCADEOIDEA FROM PRZENOSZA

The described specimen possesses the characteristic features of the genus *Cycadeoidea*: a stem of large diameter (about 35 cm.) and flower buds on short peduncles, not protruding outside the armour. The genus *Williamsonia* has, on the contrary, much thinner stems (about 10 cm.) and flower buds on long peduncles protruding outside the armour. Also the microscopic structure of our specimen is that of a typical *Cycadeoidea*.

But great difficulties arose when the relation of the *Cycadeoidea* from Przenosza to the already described species of this genus had to be established. Our *Cycadeoid* shows no diagnostic features contained in well grown flowers and mature female fructifications. Only some quantitative features of the flowers may be used.

Flowers in the male state, described by G. R. W i e l a n d, were found only on a few specimens. They may be divided into groups which differ in the size of flowers and the number of bracts. *C. dacotensis* and *R. Reichenbachiana* possess flowers about 10 cm. in diameter (including bracts), and bearing about 150 bracts. The great majority of *Cycadeoidea* fructifications bear similar quantities of bracts. But *C. Marshiana* and a few other species have flowers only about 2.5 cm. in diameter, with about 40 bracts. The *Cycadeoidea* from Przenosza having a flower 3 and 1,8 cm. in diameter and with about 40 bracts belongs to the last group.

Pollen grains were described from *C. dacotensis* from the USA, they

were present also in a flower of *C. etrusca* from Italy (G. R. Wieland, 1906: pp. 159—162), and in *R. Reichenbachiana* (G. R. Wieland, 1934, p. 105). All these specimens produced large pollen grains, about 70μ in length, while those of our Cycadeoid are small, attaining only 18μ . But several features in the flowers of the last stem show that they were not mature and therefore no conclusion considering the systematic position of the plant can be drawn from the size of the not fully grown pollen grains.

Considering the vegetative features one may find that the narrow xylem ring is characteristic. The pattern of the bundles in the leaf-bases is similar to that shown by the majority of the *Cycadeoidea* species (Text-fig. 3a₁) but sometimes there occur different ones (Text-fig. 3a) calling the double pattern of *C. polonica*.

Besides the features which may have taxonomic significance, the Przenosza Cycadeoid bears interesting pathological features, such as the abortion of most of the flower buds and in connection with this absciss layers occur in the peduncles. There are also accumulations of secretion both inside the stem and on its surface. All these symptoms are connected with damage to the plant, caused by the attack of unknown insects. The reaction of recent plants to attack by noxious insects is similar: they defend themselves by cutting off or aborting the attacked parts and by filling the damaged parts with gum, resin or an other kind of secretion.

What is more, the damage caused in this way might also have influenced the development and the size of organs which have essential taxonomic value. I shall therefore confine myself to defining the Bennettitalean stem from Przenosza as *Cycadeoidea* sp. Buckland.

CONCLUSION

1. The paper contains the description of a *Cycadeoidea* stem found in the Western Carpathians, in the locality Przenosza (Poland).

2. The specimen came in all probability from the Cretaceous strata of the Carpathian Flysch. It is shown that most probably the Barremian Verovice Beds or the dark shales of the Grodischt strata are the source of the Cycadeoids found in the Polish Carpathians.

3. Professor J. Walton's Peel Section Method was used with very good results for making microscopic preparations.

4. Both the external features and the well preserved microscopic structure make it evident that the specimen belongs to the genus *Cycadeoidea* Buckland.

5. A characteristic feature of the *Przenosza Cycadeoidea* are the flower buds which aborted their apices. Only one aborted apex is preserved.

6. Another characteristic feature of this specimen is the damage caused by insects (?) which probably was the cause of the abortion of the buds. A result of this was also the frequent secretion of „gum” on the stem and inside it.

7. From the 12 investigated buds only one bore an immature female cone, and another one microsporophylls, containing not well grown pollen, much smaller ($18\ \mu$) than the hitherto known pollen of *Cycadeoidea* (about $70\ \mu$).

8. The systematic position of the fossil could be defined only as *Cycadeoidea* sp. Buckland.

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And I would like to express my gratitude to Professor W. Szafer for generously placing the *Cycadeoidea* stem at my disposal and kindly granting all facilities for its investigation. I should also like to record my indebtedness to Professor J. Walton for help and criticism and the final correction of the paper; also to the British Council and the Polish Academy of Sciences, from which I have been in receipt of grants during the course of this work.

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STRESZCZENIE

NOWY PIEŃ BENNETYTA Z KARPAT ZACHODNICH

Treścią pracy jest opis pnia bennetyta, znalezione go w latach trzydziestych w Przenoszy w powiecie limanowskim.

Jest to piąty pień bennetyta znaleziony w Polsce. Wszystkie pochodzą z Polski południowej ze stanowisk na wtórnym złożu. Autorka wyraża przypuszczenie, że skałą macierzystą dla trzech okazów koloru czarnego pochodzących z Karpat były prawdopodobnie dolnokredowe łupki wierzowskie (barrem). Przemawiają za tym flory znajdowane w tych warstwach oraz ich występowanie w sąsiedztwie miejsc znalezienia dwóch karpackich bennetytów. Także skład petrograficzny i barwa łupków wierzowskich oraz czarnych bennetytów są zbliżone.

Okaz jest zachowany w stanie zmineralizowanym i posiada dobrze zachowaną budowę komórkową. Preparaty wykonano w przeważającej części metodą błonki (Peel Method) J. Waltona, która pozwoliła na uzyskanie wielkich preparatów i wykonanie ich serii z miejsc szczególnie interesujących. Posługiwano się również szlifami i maceracją w HF.

Praca zawiera opis budowy anatomicznej poszczególnych elementów pnia, zbudowanego z rdzenia, pierścienia łyka i drewna, kory pierwotnej oraz pancerza złożonego z nasad liści i porastających je łusek (ramentów).

Z 12 przebadanych pączków kwiatowych 2 były w stadium poprzedzającym rozwój sporofyli, 8 nie posiadało wierchołka, który został zrzuty, jak o tym świadczy zachowana strefa odcięcia, złożona z warstwy korka oraz warstwy komórek o zanikających błonach. W jednym pączku znaleziono niedojrzałe owocowanie żeńskie, a w jednym niedojrzałe mikrosporofyle.

Cechą szczególną zbadanego okazu są znajdowane w nim w wielu miejscach uszkodzenia spowodowane przez owady. Roślina reagowała na nie zrzucaniem niedojrzałych pączków kwiatowych oraz wydzielaniem gumy.

Brak dobrze wykształconych owocowań oraz daleko posunięte zmiany patologiczne w pniu są przyczyną, że autorka określając okaz z Przenoszy pod względem systematycznym ograniczyła się tylko do nazwy rodzajowej *Cycadeoidea* sp. B u c k l a n d.

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PLATES

KEY TO THE LETTERING OF THE PLATES

p = pith, x = xylem, ph = phloem, c = cortex, a = armour, b = vascular bundle, s = outer sclerenchyma zone, ca = cambium, co = cork layer, g = „gelatinous” substance, i = parts damaged by insects, l = leaf-base, r = ramenta, pa = parenchyma, m = mineral matter, cam = campanula, ov = layer of ovules and interseminal scales.

(All figures are from untouched photographs)

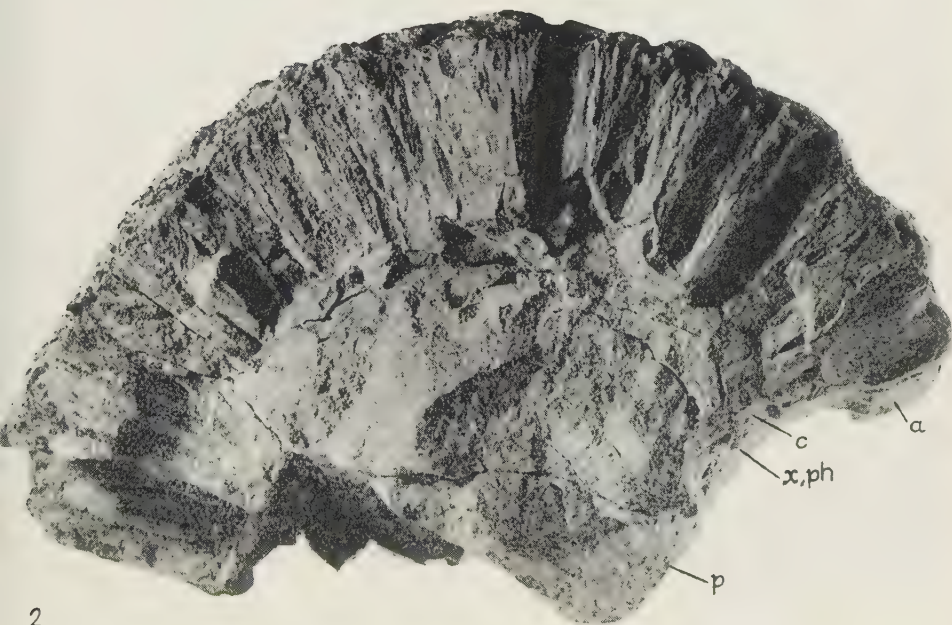
Plate I

Fig. 1. The stem of the *Cycadeoidea* from Przenosza in profile. $\times 0,4$

Fig. 2. The same stem from beneath.



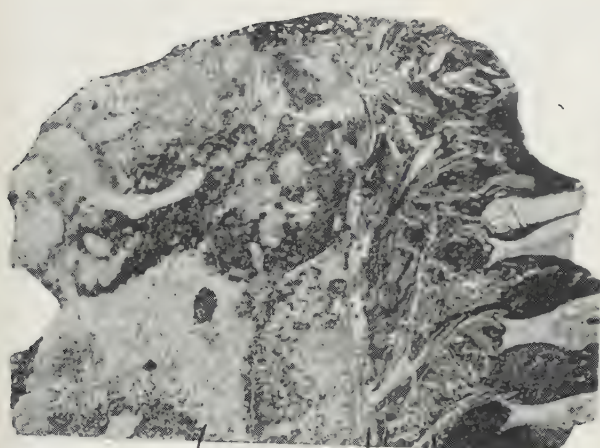
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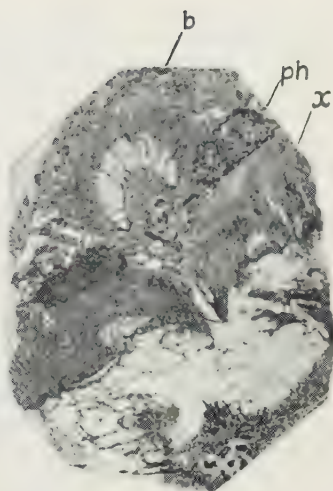
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Plate II

- Fig. 3. The apex of the stem in longitudinal section. Surface polished and etched with HF. $\times \frac{3}{4}$
- Fig. 4. A horse-shoe shaped bundle originating from the xylem-phloem ring of the stem. Ground section; $\times 2,4$
- Fig. 5. The armour of the stem in longitudinal section. The leaf-base with a cork-layer at the top. Along this layer the upper part of the leaf was cut off and shed. The ramenta are straight or wavy; Peel section; $\times 4$
- Fig. 6. Vascular strand from a leaf-base in transverse section. Peel section; $\times 33$



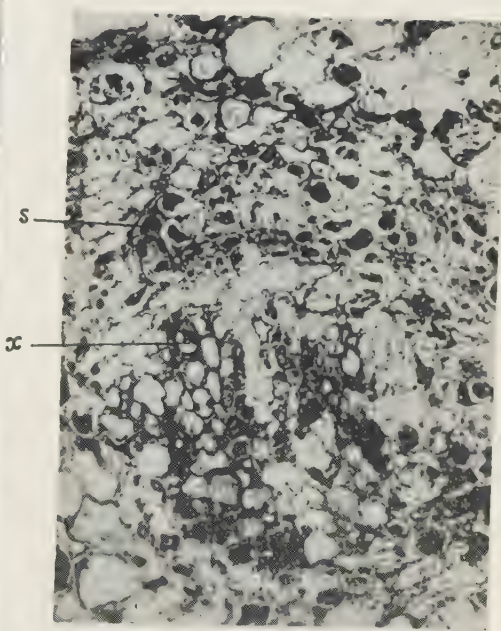
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p x,ph b a



4
b ph x



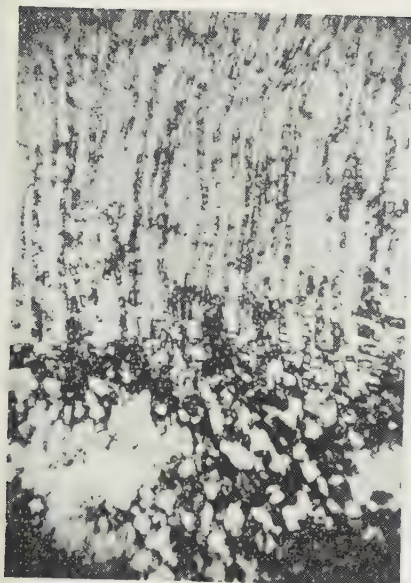
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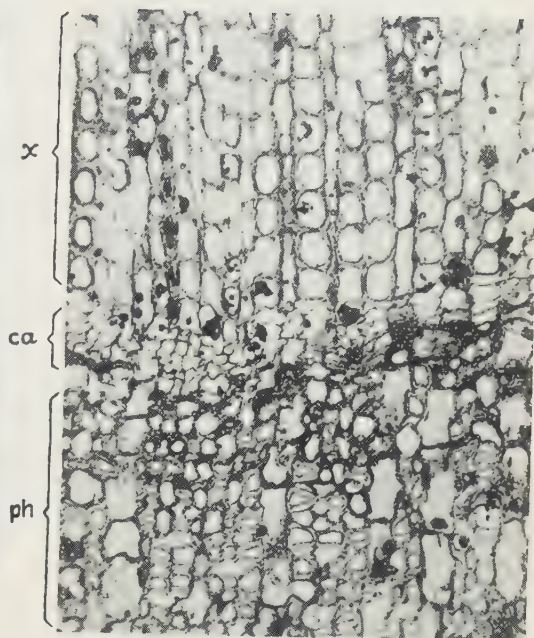
6
s x

Plate III

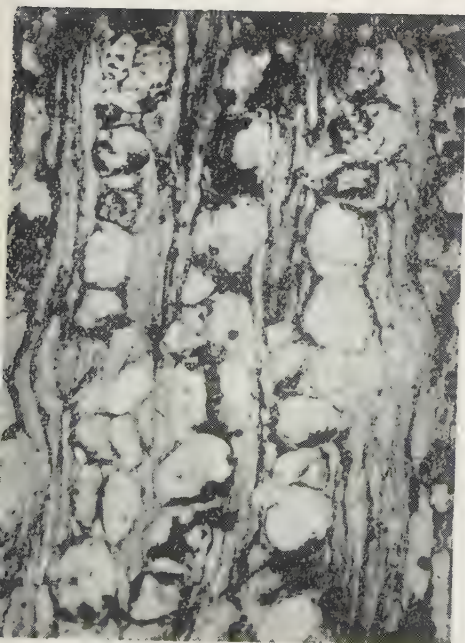
- Fig. 7. Xylem next to the pith. Peel section; $\times 20$
- Fig. 8. Transverse section through xylem, cambium and phloem of the stem. Ground section; $\times 112$
- Fig. 9. Phloem in tangential section. The elongated narrow phloem elements and the oval, wide cells of the medullary rays are visible. Peel section; $\times 112$
- Fig. 10. Xylem of the stem in radial section with elongated flat pits, round pits and intermediate forms of pits. Peel section; $\times 112$



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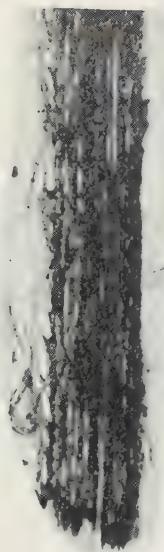
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Plate IV

- Fig. 11. Fragment of a single ramentum, isolated by using maceration in HF; \times 28
Fig. 12. Fragment of a ramentum bearing filamentous outgrowths. \times about 32
Fig. 13. Fragment of a ramentum seen under big magnification, showing filled and empty outgrowths. \times 160
Fig. 14. „Gum” ducts in the pith of the stem. Peel section; \times 48
Fig. 15. Ramenta in transverse section. Peel section; \times about 48



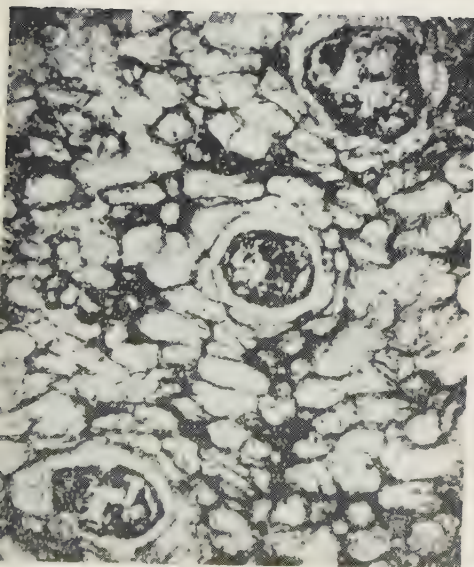
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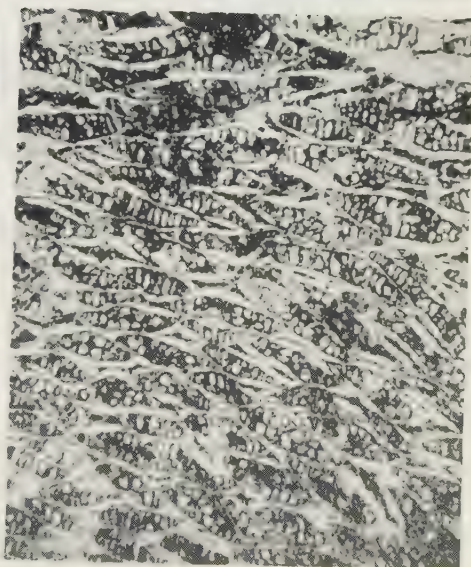
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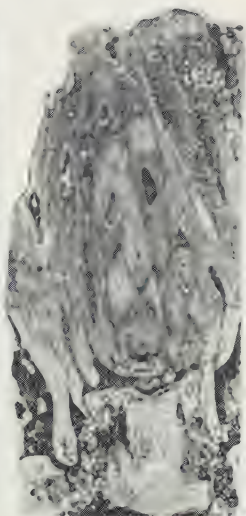
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Plate V

- Fig. 16. Bud V which has aborted its apex, in longitudinal section. Peel section; $\times \frac{4}{5}$
Fig. 17. Bud VI in longitudinal section. Peel section; $\times \frac{4}{5}$
Fig. 18. The apex of bud V in longitudinal section on another preparation. Peel section; $\times 2$
Fig. 19. The apex of bud VI in longitudinal section. Peel section; $\times 2$
Fig. 20. Cork-layer from the upper part of the peduncle V. Peel section; $\times 28$
Fig. 21. Secretion on the top of peduncle V. Peel section; $\times 28$



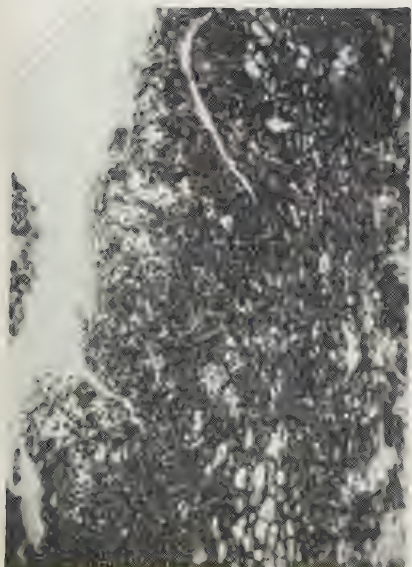
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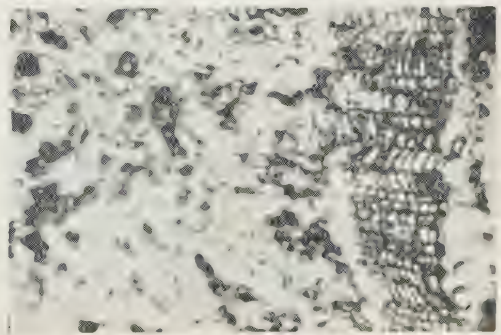
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Plate VI

- Fig. 22. The rim of the top of peduncle V in longitudinal section, showing the torn edge. Peel section; $\times 20$
- Fig. 23. The upper part of bud XI in transverse section. Peel section; $\times \frac{4}{5}$
- Fig. 24. The peduncle of bud XI in transverse section, showing parts damaged by insects. Ground section; $\times 4$
- Fig. 25. Bud XI in longitudinal section. Peel section; $\times 2$
- Fig. 26. Pitted elements from the xylem of the vascular strands of bud V. Peel section; $\times 160$

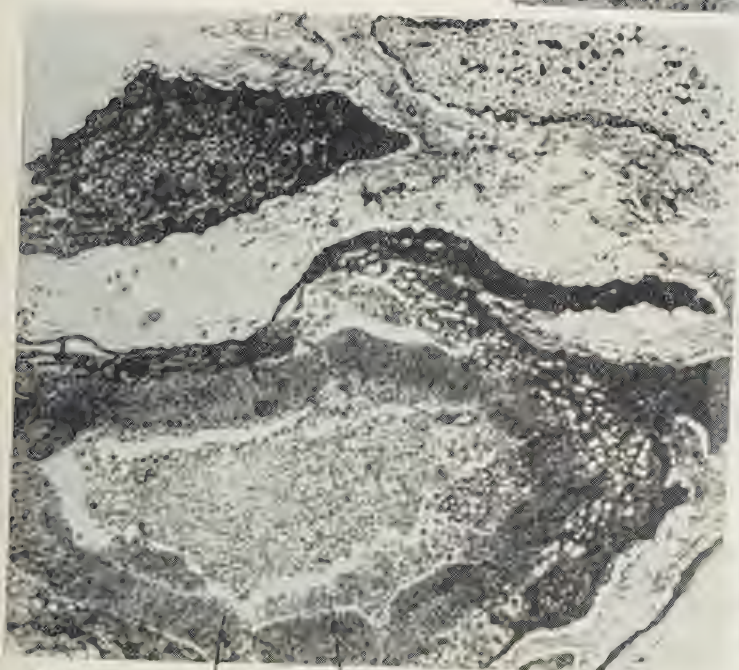


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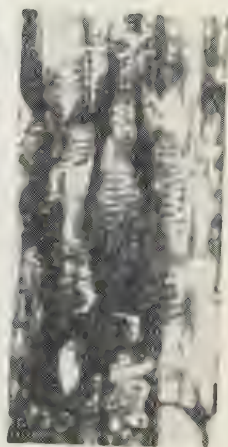
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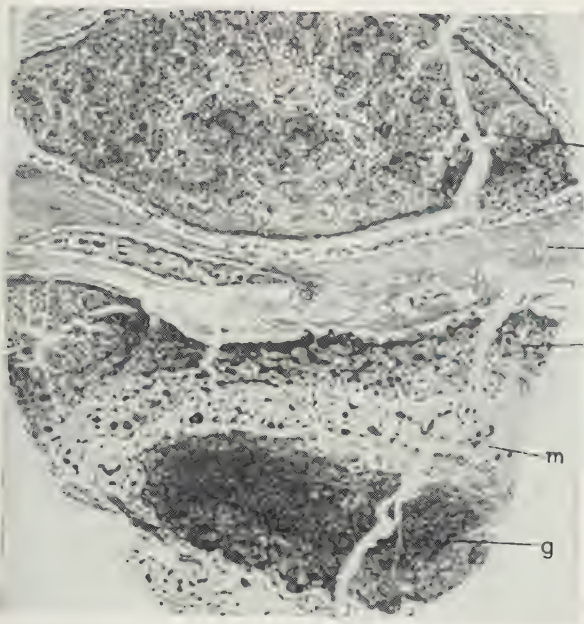
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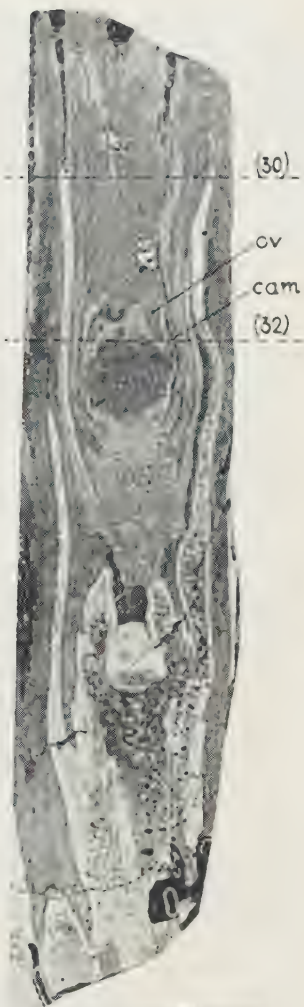
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Plate VII

- Fig. 27. Peduncle IX in transverse section; $\times 4$
- Fig. 28. Bud XV in longitudinal section. At the bottom the peduncle, above the aborted bud containing a female cone, succeeded by the part destroyed by insects. The horizontal lines mark the position of sections seen on figs. 30 and 32. Peel section; $\times 1,6$
- Fig. 29. The middle part of bud XV, containing the female cone. Peel section; \times about 2,4
- Fig. 30. The upper part of bud XV in transverse section. The bud filled inside with scattered fragments of tissue resulting from feeding of insects. Ground section; $\times 2$



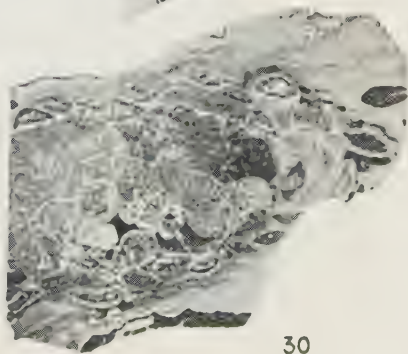
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Plate VIII

- Fig. 31. Longitudinal section of bud XV a few mm. from the section on fig. 28.
Peel section; $\times 1,6$
- Fig. 32. The female fructification in transverse section. Ground section; $\times 4$
- Fig. 33. Magnified fragment of the preparation seen on fig. 32. Ground section; $\times 28$
- Fig. 34a. An internal bract of bud XV in transverse section. Ground section;
 \times about 40
- Fig. 34. Bract in longitudinal section. Peel section; $\times 20$

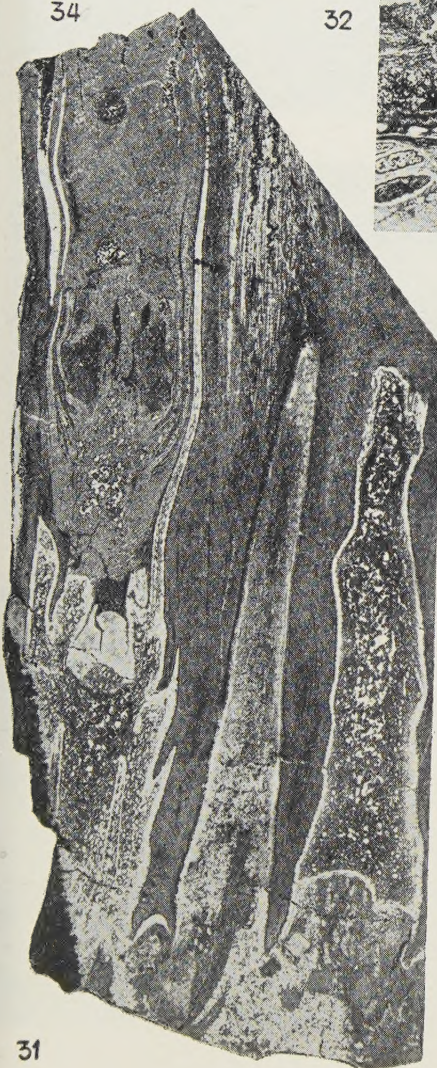


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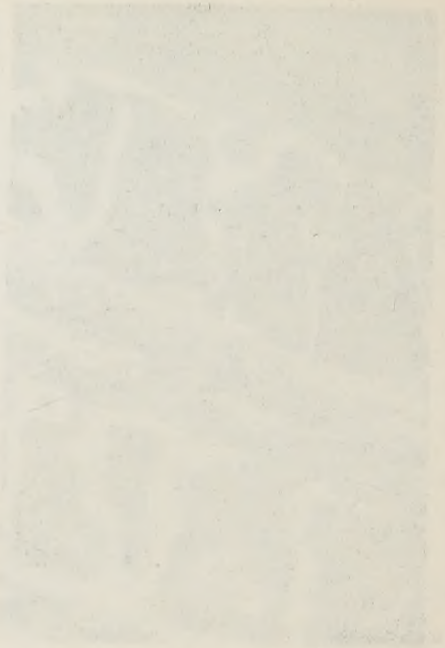
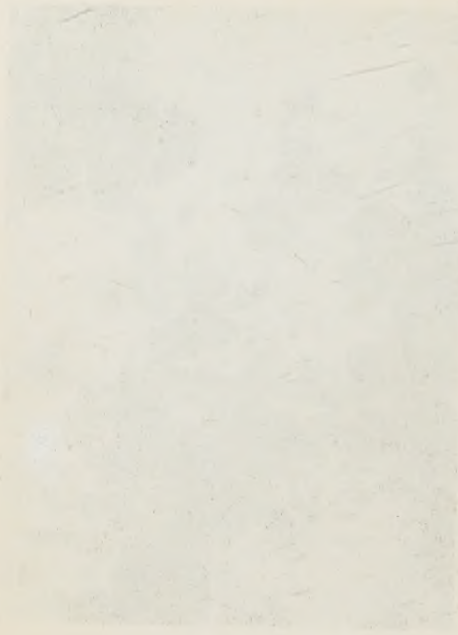
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34a



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